

Neurophysiological correlates of the recognition of facial expressions of emotion as revealed by magnetoencephalography

M. Streit ^{a,*}, A.A. Ioannides ^b, L. Liu ^b, W. Wölwer ^a, J. Dammers ^b, J. Gross ^b, W. Gaebel ^a,
H.-W. Müller-Gärtner ^c

^a *Department of Psychiatry, University of Düsseldorf, Bergische Landstrasse 2, D-40605 Düsseldorf, Germany*

^b *Institute of Medicine, Research Centre Jülich, D-52425 Jülich, Germany*

^c *Department of Nuclear Medicine of the University of Düsseldorf at the Research Centre Jülich, D-52425 Jülich, Germany*

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Abstract

MEG correlates of the recognition of facial expressions of emotion were studied in four healthy volunteers. Subjects performed a facial emotion recognition task and a control task involving recognition of complex objects including faces. Facial emotion recognition activated inferior frontal cortex, amygdala and different parts of temporal cortex in a relatively consistent time sequence. The characteristics of these activations were clearly different from those recorded during the control task. Most interesting was the fact that faces evoked different MEG responses as a function of task demands, i.e., the activations recorded during facial emotion recognition were different from those recorded during simple face recognition in the control task. These findings support the assumption that MEG is able to specifically identify the activation pattern of the brain when recognition of the emotional expression of a face is performed. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Recognition of facial expressions of emotion is one of the most relevant communication skills in humans and non-human primates. Furthermore, it is one of the first communicative abilities in human life, that occurs much earlier in childhood than for instance the faculty of speech. Therefore it develops in a relatively early stage of brain maturation, while the process of establishing the hard-wiring of neurons is very intensive. The neural representation of facial affect recognition is thought to be mediated by a multiplex circuitry [9] that is partly independent of neural systems that extract other, non-affect related, information from faces [6], e.g., the individuals identity or sex [8,45].

There is strong evidence from animal studies [10,33,39,41,48], psychological experiments with brain lesioned patients [20,53] and functional neuroimaging studies with PET [16,29,46,49] and fMRI [28,42] in healthy

humans that faces are very effective stimuli, that evoke strong responses in the brain both in terms of activity of individual neurons, and of regional specificity across the cortical mantle.

Optical imaging studies [51] have shown that neurons responding to related facial features are grouped into clusters around 1 mm in size. If the spatial proximity of similarly sensitive cells is also reflected in the cell orientation, then the activity from such assemblies is well capable of producing an electrophysiological signal which is measurable. Evidence for that assumption has been provided by Allison et al. [3] who found face selective negative potentials on the surface of the fusiform and inferior temporal gyri by means of intracranial EEG recordings in humans. Also EEG recordings on the scalp surface revealed face selective event-related potentials over the posterior temporal scalp [14]. Magnetoencephalography has been used in two studies of human face perception so far. By means of passive stimuli viewing designs Lu et al. [37] and Sams et al. [44] reported strong neuromagnetic responses to face-stimuli in comparison to other simple and complex objects over occipitotemporal brain regions.

* Corresponding author. Fax: +49-211-922-2021; E-mail: streit@uni-duesseldorf.de

Clues to the neural basis of the recognition of facial expressions of emotion have also been obtained through studies with non-human primates. Neurones firing selectively during the presentation of facial expressions and other complex stimuli with social and emotional significance have been observed in different inferior frontal areas [52], in the extrastriate visual cortex [19], and in the amygdala [5,39]. Studies with brain lesioned humans also seem to favor inferior frontal cortex [20,30,53] and different temporal areas [2] as main candidates for the expression recognition process in humans. The amygdala seems to play a particular role in the recognition of fearful expressions [1].

Cerebral blood flow studies have suggested that also in healthy humans the inferior frontal cortex [12], the amygdala [37,38], the middle temporal gyrus and the fusiform gyrus [45] as well as the right anterior cingulate are activated during recognition of facial expressions. Results of two EEG studies [32,50] were inconsistent showing different patterns of event-related potentials as a response to emotional faces. This might be due to different stimuli characteristics, task designs, or analysis strategies of the data.

The findings reviewed above indicate that recognition of facial expressions of emotion is a process depending on the activity of several brain regions. Although much effort has already been made, we are just beginning to develop methods addressing directly the key questions: which brain areas contribute to the process, when and how these areas interact, and whether those contributions are based relatively more on perceptive, mnemonic, or emotional functions. We reasoned that knowledge of the spatio-temporal organisation of activity can provide valuable insights.

The purpose of our study was to attempt to extract such a spatio-temporal description, directly from the MEG signal recorded during the execution of face recognition and facial emotion recognition tasks. MEG combines high resolution in time, with reasonable precision in localisation [18]. In terms of response and recording sampling rate the MEG signal offers, at least in theory, the possibility of identifying the spread of activation into different brain areas. To our knowledge MEG has not been reported in studying emotion recognition as yet. This is not too surprising; while a temporal resolution of a millisecond is

routinely available, the disentangling of spatially distinct, but temporally overlapping generators requires more sophisticated analysis than the routinely used methods. To achieve this we have used Magnetic Field Tomography (MFT) [21,24], a method which can handle focal as well as distributed activity, with no prior assumptions about their form.

We have recorded magnetic fields during a facial emotion recognition task and additionally, during a simple face and object recognition task as a control condition, so that we can differentiate responses which are evoked specifically by the recognition of emotional expression in faces. The design of the study was guided by previous work, where a difference was identified in the EEG signal between face affect and simple face recognition [47]. The first question to address is whether or not MEG can detect regionally specific activations which differentiate between the two cases. As we will demonstrate our MFT results provide a positive answer to this basic question, paving the way for more detailed studies which are now under way.

2. Methods

2.1. Subjects

Four right handed male volunteers (mean age = 30, 25 years, range = 24 to 35) without history of psychiatric or neurological disorder participated in the study. Alcohol/substance abuse or use of psychotropic medications was excluded. The study was approved by the local university ethics committee.

2.2. Experimental tasks

2.2.1. Task 1 (face and object recognition)

Black and white photographs of faces from Ekman and Friesens set of pictures of facial affect [11] together with photographs of the following five categories of living and non-living objects served as stimuli: front views of lorries, chairs and horse heads together with birds and flowers (Fig. 1). The selection of the stimuli has been partially influenced by previous published studies but considerations of compatibility have also been used. Like faces, all



Fig. 1. Examples of the stimuli used in the experiments.

stimuli should have a more vertical than horizontal extension. All stimuli had to contain features (e.g., eyes, nose, mouth in faces) which might be important for the coding process. The object categories had to allow unambiguous semantic classifications. Thirty different images per object category have been used. The photographs have been digitized and the general visual qualities of the pictures have been digitally reworked to ensure uniformity. A luminance meter was used to adjust the images to natural daylight conditions in rooms (average luminance of 30–40 cd/m²). Finally they have been mounted into the centre of the same mid grey background to ensure uniform figure/ground contrasts. Stimuli subtended a visual angle of about $6 \times 4^\circ$. They were presented in random order for 500 ms on a screen. Subjects were instructed to give the response through selection from a multiple-choice list containing the six object-categories (including faces). The list appeared on the screen with a delay of 1 s to avoid confounding motor effects.

2.2.2. Task 2 (Facial affect recognition)

Only the faces from task 1 served as stimuli. Each of the five faces displayed the six basic emotions of happiness, fear, anger, surprise, disgust and sadness. Stimulus-presentation time and general task design were equivalent to task 1, but now subjects were instructed to judge the facial expression through selection from a multiple-choice-list containing the six basic emotions.

2.3. Data acquisition and signal processing

Magnetic fields were recorded simultaneously over the left and right fronto-temporal areas (Fig. 2) using the BTi

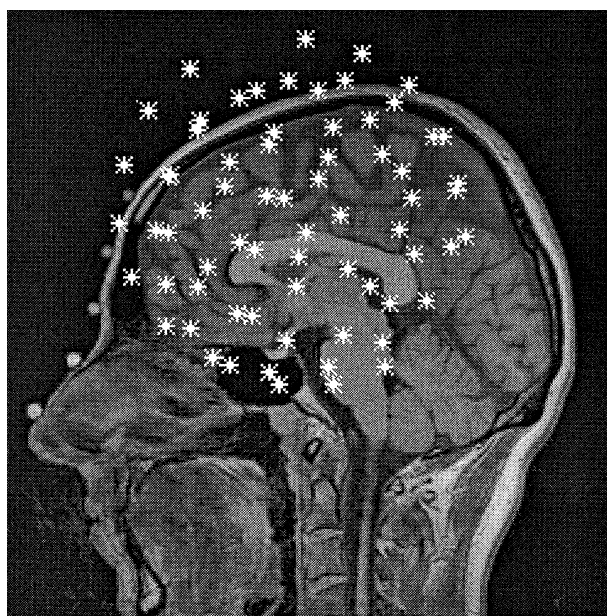


Fig. 2. Placement of the MEG sensors used in the experiment with the twin-system during run 3.

twin MAGNES system (2×37 channel) in three separate runs. In run 1 the MEG was recorded during task 1 (face and object recognition); in runs 2 and 3 the MEG was recorded during task 2 (facial-affect recognition). The same dewar position was used for the first two runs, but for the repetition of the affect-recognition task (run 3) the dewars were moved to a more frontal position. The first two runs provided the contrast between face and object vs. face affect recognition tasks, under identical conditions (except for task difficulty which we did not control for). The dewar placement in the final run was chosen to enhance the chance of identifying activity from frontal and mesio-frontal generators; the extra run also provided a very useful replication test for the affect condition.

Subjects were in a magnetically shielded room, stimuli were back-projected onto a screen via an optical stimulus delivery system with an optical fibre cable providing the link between the computer generated images in the unshielded environment and the screen inside the shielded room.

The experiment was repeated with one of the subjects using the 148 channel whole-head system to test consistency of the previously observed activations recorded with the twin system. Furthermore the new system provided the opportunity to record activations in occipitotemporal and parietotemporal brain regions, that had been relatively far away from the sensors in the twin experiment. The activation of deep generators produces a weak signal which is distributed over a wide area; it is therefore much easier to capture signals of deep activity with the Whole-Head-System.

The neuromagnetic signals were sampled at 1 kHz. After removing artifacts and filtering (DC–45 Hz), the signals were averaged for each object category of run 1 and for the sets of emotional faces of runs 2 and 3. Epoch length was 1.2 s, starting 200 ms prior to stimulus onset. A baseline was computed from the average of 200 ms pre-stimulus MEG signal, and subtracted from the post stimulus interval. A digital mask was traced for each subject prior to the experiment, with fiducial points used to define the MEG coordinate system. The same fiducial points were identified in each individual MRIs by placing vitamin pills which were clearly identifiable in the MR images. It was therefore possible to relate the MEG coordinate system to the MRI based coordinate system and to superimpose the MEG source estimates on each individual MRI.

2.4. Data analysis and source localization

The averaged MEG signals for each subject, run and condition were applied to MFT analysis. MFT uses a one step iteration algorithm to extract probability estimates for the primary current density within a well defined source space. The algorithm has two sets of adjustable parameters: one set which defines the compromise between good

resolution and low sensitivity to noise and a another set which defines how the preferential sensitivity to superficial sources is moderated. All adjustable parameters are fixed by a training session with computer generated data, so no free parameter remains when the real data are handled. The basic model assumption is that the direction (not the full vector) can be expressed by a linear sum of lead fields modulated by a scalar function of position (which is fixed by training). The logical and algorithmic steps are described in detail elsewhere [26]. Recent theoretical considerations [48] have shown that MFT has the optimal stability properties amongst the many non-linear schemes that can be defined. This confirms a similar conclusion reached earlier on the basis of tests with computer generated data [21]. Furthermore, MFT has been repeatedly applied to the analysis of real MEG data [27]. It has successfully identified activity in simple cases where focal activations are expected; in such cases the location of maximum MFT activity coincided with the location of single current dipole solutions, for both superficial [22,25] and deep generators [4,23–25]. More pertinent to this study is the capability of MFT to identify the foci of high activity when the generators are distributed as demonstrated with computer generated data [21], the analysis of MEG data from a pair of implanted dipoles in humans [24] and in numerous other studies with real data [35,43].

Separate MFT analysis were made for the left and right dewar signals. For each MFT analysis the primary current density was confined to a source space covering the brain hemisphere on the side of the active dewar, but the full current density was modelled by a spherical conductivity profile. Separate models were used for each dewar, with the centre of the conducting sphere chosen in each case as the best sphere fit to the inner skull outline below the active sensors. Typically the sphere centre fall 1 or 2 cm on the opposite hemisphere. The source space, i.e., the region of space where non-zero primary currents could exist, was a spherical section chosen so that it described best the cortical outline on the side of the active dewar, and extending to the brain midline. In this way the full brain area was covered by the combined left-and-right source spaces, but the most reliable estimates were, of course, obtained from the part of the source space directly below the sensors. The areas of least sensitivity were therefore the occipital and superior prefrontal areas of the brain, with an improved, but not optimal coverage of the prefrontal areas during run 3. The incomplete sensor coverage, as well as the use of gradiometers in the twin system limit the sensitivity to deep activity; both drawbacks are eliminated when the measurements are made with the full head system.

We identified regions of high activity by automatic searches millisecond by millisecond through the MFT source space. To be cautious, only the strongest activations (at least 90% of the estimated current density at a given latency within the source space) were selected. The brain

areas where those maximum activations occurred were labelled as regions of interest (ROI). A comparison of activations within a ROI across two runs at a given latency was only rated as significantly different, if the estimated current density was at least 50% stronger in one of the runs.

3. Results

3.1. Behavioral results

The four subjects scored between 60% and 93% accuracy (mean number of correct answers = 21, 38, S.D. = 4, 24) in task 2 (runs 2 and 3), showing that the emotional expression of the faces was correctly recognized by all of the subjects high above chance level (approximately 17% in a six-alternative choice). Subjects did not show significant differences of behavioral performance between the two repeated runs of task 2 (run 2: mean number of correct answers = 21, 5, S.D. = 4, 43; run 3: mean number of correct answers = 21, 25, S.D. = 4, 72).

3.2. MEG recordings with the twin system

To study brain responses specific to facial expression recognition neuromagnetic fields recorded during the presentation of faces in run 1 (simple face recognition) were compared to fields recorded during the presentation of faces in runs 2 and 3 (emotion judgement). In all of the four subjects particular temporal and frontal areas responded stronger to faces in both runs 2 and 3 when expression recognition was required. Then, 140–170 ms after stimulus onset, an area in the posterior sector of right superior temporal cortex was the first one that responded significantly stronger to face affect judgment than to simple face recognition. This was observed across all of the four subjects during both runs 2 and 3. Furthermore, this area was consistently reactivated between 220 and 250 ms and, less consistent between 450 and 530 ms (S1, S3 and S4). The next region that responded preferentially to facial affect was in the middle sector of right temporal cortex at 180–210 ms. This activation was observed in 3 of the 4 subjects (S1, S2, S4), but a second activation followed slightly later in the same region at 210–240 ms in all of the subjects (Fig. 3). It was stronger and slightly earlier in run 2 than in run 3. In two of the subjects (S2, S4) two further activations appeared around 370 ms and 520 ms. In the left hemisphere first activity selective to the affect recognition task occurred in the middle sector of temporal cortex at 210–270 ms. This neuromagnetic response was consistent across the four subjects and occurred in both affect recognition runs. It was followed through an activation of left inferior frontal cortex at 230–300 ms (Fig. 4). In three of the subjects (S2, S3, S4) inferior frontal cortex was reactivated around 350 ms and partly later. Also the

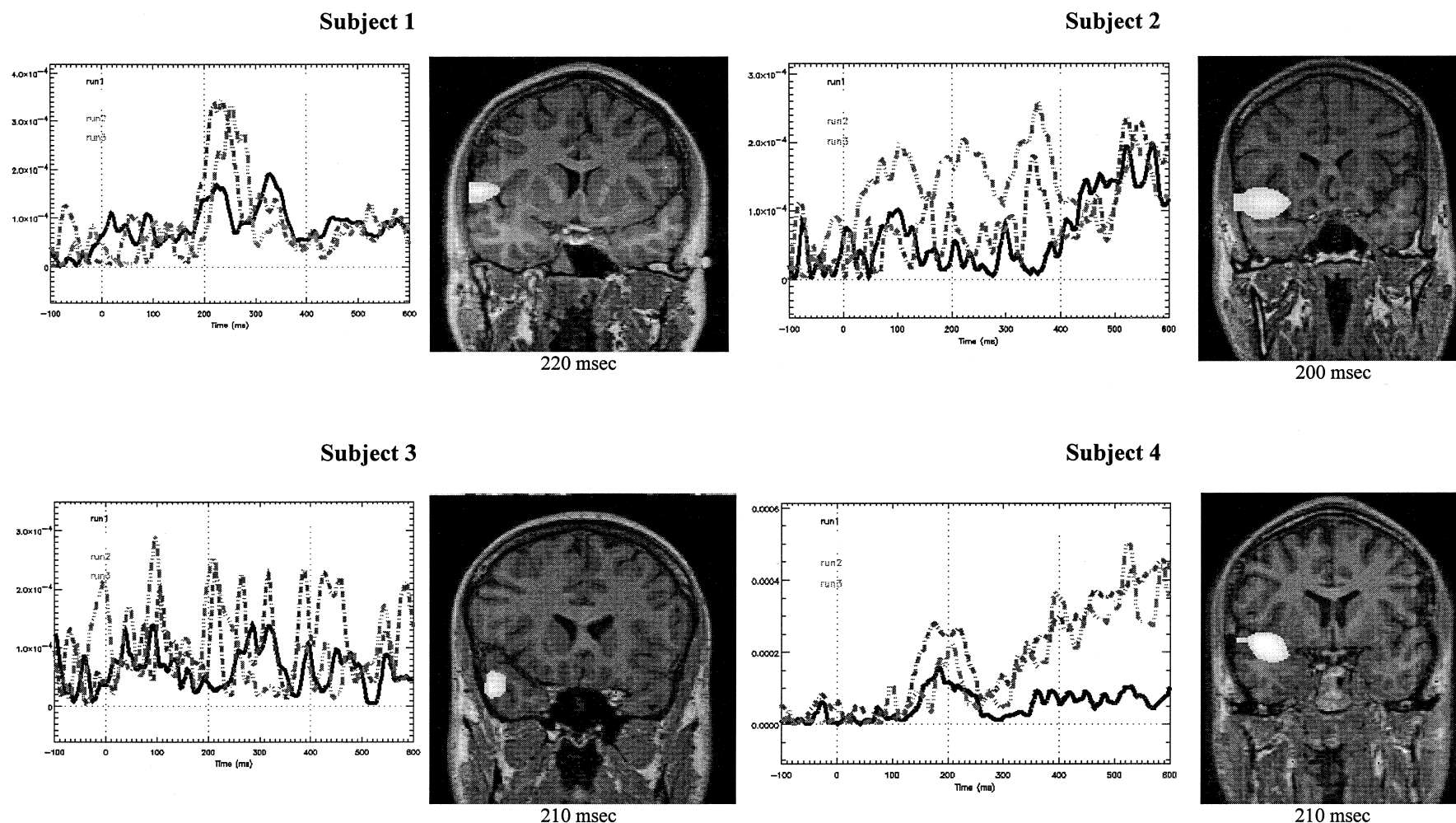
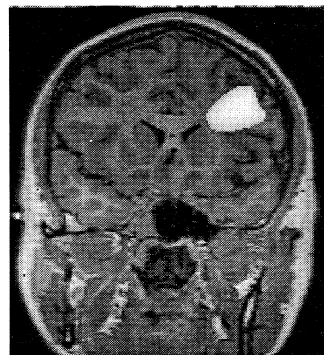
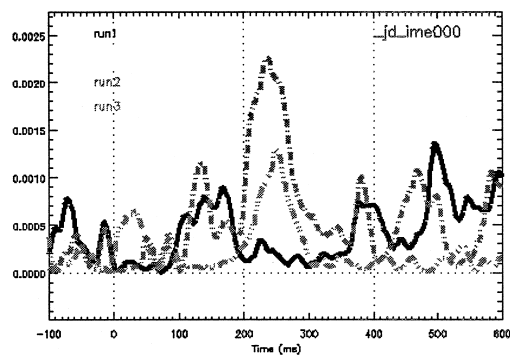


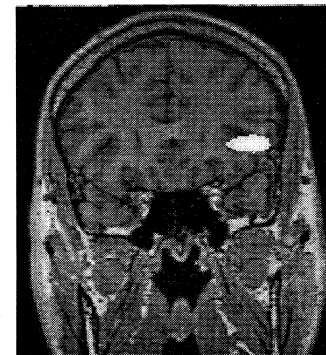
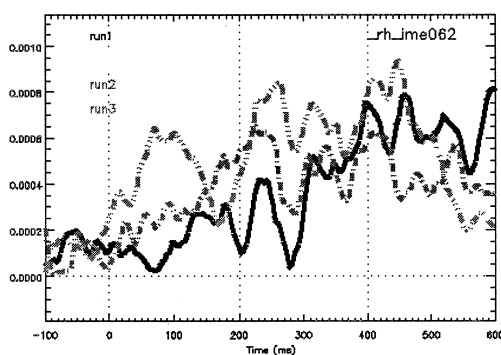
Fig. 3. Activity in the middle sector of right temporal cortex during the presentation of faces. The activation curves show activity in that brain area plotted against time. The solid black line displays activity recorded during simple face recognition (run 1), the dotted lines during recognition of facial expressions of emotion (run 2 = dark grey, run 3 = mid grey). The MRI overlays display the area of maximum brain activity within 200 and 220 ms during run 2.

Subject 1



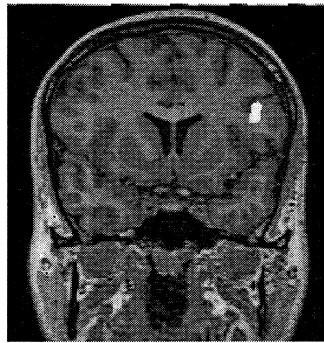
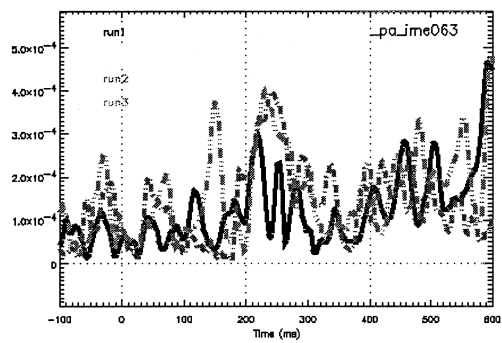
240 msec

Subject 2



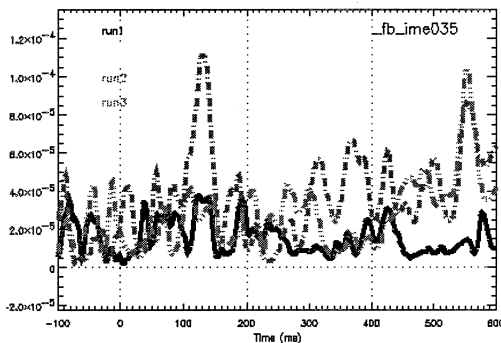
240 msec

Subject 3



240 msec

Subject 4



270 msec

Fig. 4. Activity in left inferior frontal cortex during the presentation of faces. The activation curves show activity in that brain area plotted against time. The solid black line displays activity recorded during simple face recognition (run 1), the dotted lines during recognition of facial expressions of emotion (run 2 = dark grey, run 3 = mid grey). The MRI overlays display the area of maximum brain activity within 240 and 270 ms during run 2.

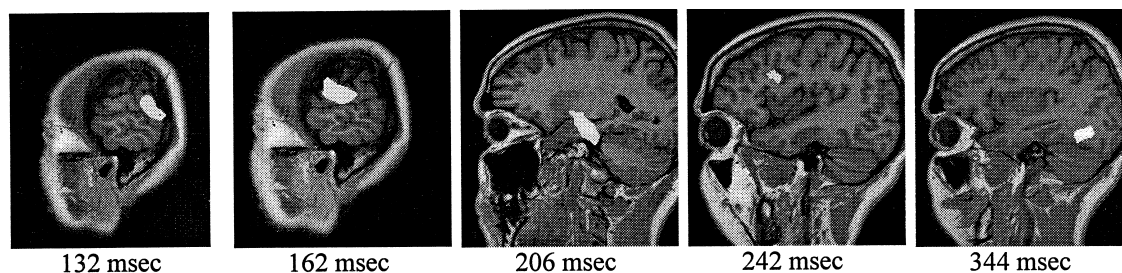


Fig. 5. Time sequence of brain activations during the recognition of facial expressions of emotion (run 2) recorded with the twin system in subject 1.

right amygdala showed selective activity during facial expression judgement, but this was only consistent in S1 and S2 across both affect runs (latency at about 220 ms). In S3 only in run 3 a strong activation was observed and in S4 the activations occurred with a relatively similar strength in all of the three runs.

The areas were activated in roughly the following time sequence (Fig. 5): (1) posterior sector of right superior temporal cortex, (2) middle sector of right temporal cortex, (3) right amygdala, (4) posterior sector of right superior temporal cortex approximately together with middle sector of left temporal cortex, (5) left inferior frontal cortex, (6)

Subject1

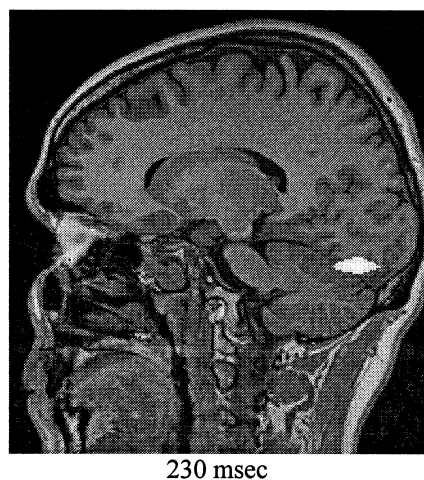
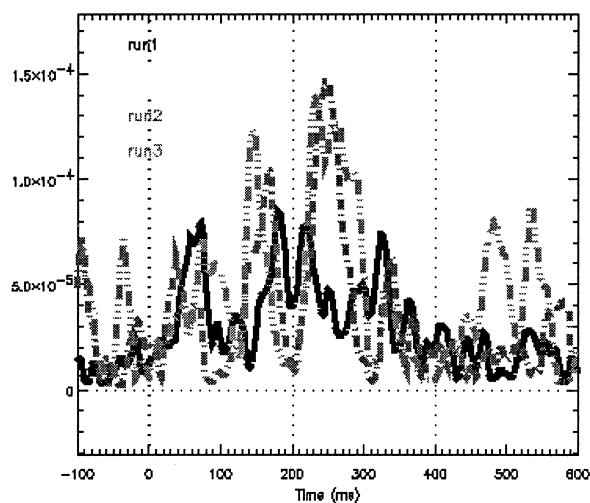
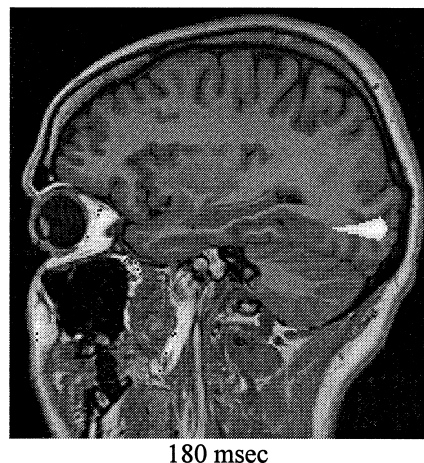
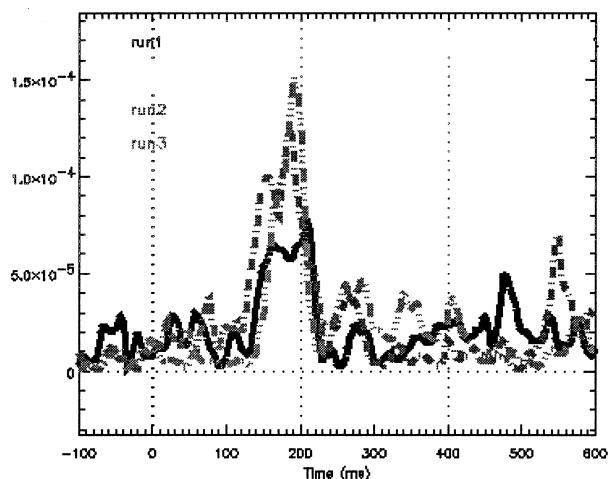


Fig. 6. Posterior activations recorded with the whole-head system during the presentation of faces in the repetition of the experiment in subject 1. Activation curves display activity plotted against time in occipitotemporal cortex (upper graph) and in lingual/fusiform gyrus (run 1), the dotted lines during the recognition of facial expressions of emotion (run 2 = dark grey, run 3 = mid grey). MRI overlays display the area of maximum brain activity at the indicated latencies in run 2.

further reactivations of the temporal and left inferior frontal structures. However, as described above, this sequence is not completely consistent in all of the subjects. An additional characteristic of a spatio-temporal activation pattern occurred in the left hemisphere. Activity during affect recognition in the anterior temporal cortex slightly preceded activity in the inferior frontal cortex. This was identified during runs 2 and 3. In the right hemisphere the activity in posterior temporal cortex preceded activity in middle temporal cortex, but occurred later again.

In the course of repetition of tasks performed during runs 2 and 3 consistent changes of current source densities or latencies of activations were not observed across runs.

A comparison between the recordings during the recognition of faces and during the recognition of other complex objects revealed a region in right superior temporal cortex that responded preferentially to faces in all of the four subjects at about 100 ms and at 170–220 ms. Additional face selective responses have been observed in this area at later latencies in three of the subjects (S1, S2, S3). Activity in some extra-striate visual areas starting at about 70 ms after stimulus onset was evoked by all object-classes of task 1. Bilateral activity was observed between 70 and 150 ms in posterior parts of the superior temporal cortex, in posterior parts of the middle temporal gyrus and in a posterior ventral area of the temporal cortex covering parts of lingual and fusiform gyri. These areas became active a second time between 180 and 230 ms.

3.3. MEG recordings with the whole-head-system

The repetition of the experiment with one of the subjects (S1) revealed additional areas that responded preferentially during expression recognition compared to simple face recognition. One of those activations was located in inferior occipitotemporal cortex, with a first peak at about 180 ms, and a second one at about 250 ms (Fig. 6). An area covering posterior fusiform and lingual gyri regions responded at about 130–160 ms and again at about 230 ms (Fig. 6). This area additionally responded to faces at other latencies across all of the 3 runs. Regions covering right anterior cingulate gyrus (at about 230 ms) and an area in right middle orbital cortex (220 to 240 ms, 380 ms) became also preferentially active during facial affect recognition. Additionally to right amygdala also left amygdala responded preferentially to emotional faces at about 280 ms in both runs 2 and 3 in the repetition of the experiment. Activation in left inferior frontal cortex now only occurred once at about 260 ms. Face selective responses have been observed again in task 1 in right superior temporal gyrus at about 130 ms and at about 180 ms.

4. Discussion

We have provided evidence that MEG is able to identify neural activity that is crucially involved in the decod-

ing of facial expressions of emotion. Furthermore we have shown that this activity is separable from activity, that is devoted to simple perception of faces. Brain activations following affect recognition and simple face recognition differed in three basic ways: (1) an area was activated during affect recognition, but not at all during face recognition; (2) an area was activated through both task conditions, but the strength of activation during affect recognition was much higher; (3) an area was activated through both task conditions at an early latency, but a later reactivation was only present during the affect condition. Therefore, facial emotion recognition compared to simple face recognition introduced either new, enhanced or repetition of brain activity.

Our MFT analysis has identified the following areas as key players in the processing of facial emotion recognition: the posterior sector of right superior temporal cortex, the right inferior occipitotemporal regions, the middle temporal cortex bilaterally, the amygdala, the left inferior frontal cortex, and the right anterior cingulate gyrus region. These brain regions have already been identified to be involved in the processing of faces and/or emotion related information in previous brain imaging studies. However, MEGs high resolution in time allows us to make first assumptions about the time course of activation within the neural network specifically underlying facial expression recognition. The earliest activations preferential to the emotional content of faces appeared in the posterior sector of superior right temporal cortex and in inferior occipitotemporal cortex at about 160 ms after stimulus onset. The localization of the first mentioned brain region is in agreement with findings of a recent facial affect recognition study [2] in brain lesioned patients. Therefore, our results provide further support for the assumption that relatively early areas of the visual processing stream play a role in emotion recognition [31]. Whether this role is based on initially existing re-entrant mechanisms probably via backprojections from high-order visual areas or whether it emerges in the course of repeated stimulus presentations as a result of a priming effect might be clarified through single-trial analysis.

An area in the middle sector of temporal cortex (Fig. 3) was the next brain region that responded preferentially in the affect recognition task. Because of its numerous anatomical connections with other areas of both visual streams [49] this region is well prepared to play an essential role in the analysis of complex facial information, in particular in the recognition of emotional expressions [45]. In our study this area was activated bilaterally, but not simultaneously in the two hemispheres. In all of the subjects it was activated first in the right hemisphere at about 200 ms. The corresponding region in the left hemisphere was activated 20 to 60 ms later. This finding, together with the fact that only the right posterior temporal regions showed affect selective responses supports the claim made by different authors [15] that the right hemisphere has

some advantages over the left in performing difficult face and emotion processing tasks. Again, in both hemispheres, reactivations occurred, with the special feature of the right temporal cortex to show a rapid reactivation within 20 to 30 ms after the first one. This might be a local network process providing retrieval of stored expression-related information.

The amygdala region became active during facial emotion recognition 20–40 ms after the middle temporal areas. This finding confirms numerous reports about the role of the amygdala in the evaluation of social and emotional significance of incoming sensory information. Furthermore, this area has been proposed to be a central part of a system that integrates emotion and memory [34], a function, that is certainly important for facial expression recognition. Although activity from the amygdala was expected to be present during the facial affect recognition task, a reliable neuromagnetic correlate of this activity was not guaranteed, partly because of the small size of the amygdala, and partly because of its deep location. This may well be the reason why the activity was not consistently observed across the four subjects, especially with the twin system. Evidence for enhanced sensitivity to deep sources of the new whole head system was obtained through the repetition of the experiment in one of the subjects. While measurements with the twin system only showed preferential activation during emotion recognition in the right amygdala, measurements with the whole-head-system revealed activity in regions of both left and right amygdala.

Responses from an even deeper area covering right anterior cingulate, occurring at about 240 ms after the onset of the stimulus for the affect recognition task, were only identified from MEG signals recorded with the whole-head-system. This area has often been referred to be critically involved in regulating the emotional state in response to sensory stimuli [13]. Our experiment was not designed to engender emotions in the subjects. However, the possibility that our facial stimuli did so, cannot be excluded.

Left inferior prefrontal cortex was the last area to initiate its participation in the affect recognition process. Areas of this region have been reported in previous brain imaging studies with emotional stimuli but their role is not unambiguously clarified. Whether the activity in these regions is due to a perceptual processing level [49], to the engendering of emotional feelings [13,40], to processes like decision making (i.e., which emotion has been expressed by the face) and working memory [7,17], or specifically to the evaluation of emotional information faces content is still under discussion. The possibility that we might have induced emotions with our facial stimuli has already been mentioned above. On the other hand, it is very probable that a complex process like facial expression recognition needs an organizing mechanism like the one described in the working memory concept, since a spatio-temporal pattern of brain activation needs to be maintained

and the different perceptual and memory-related neural components need some coordination. Nevertheless, the results of a recent PET study of George et al. [12] subserve the assumption that inferior prefrontal cortex indeed shows some specificity to the evaluation of incoming emotional information. When activity measured during facial identity recognition was subtracted from activity measured during facial expression recognition regions in inferior prefrontal cortex remained significantly activated, although both tasks included a comparable load on working memory. Also Lane et al. [31] reported strong contributions of prefrontal cortex to the processing of emotional stimuli in comparison to different control conditions.

An explanation of those somehow conflicting reports would be that the repeated activations we measured in left prefrontal cortex might represent different processing stages of the affect judgement process, each of them relatively more related to psychologically defined categories like perception, working memory, recall, emotion recognition or regulation of emotion. This is in agreement with assumptions of Haxby et al. [17]. The authors concluded that left prefrontal areas initially perform operations that are associated with initial encoding of the face, and thereafter rely on the maintenance of working memory operations which in turn entail more elaboration of associations, such as making judgements about facial expressions.

Our study is a first tentative step in the identification of the spatio-temporal sequences of brain activations associated with facial affect recognition. The results provide useful insights, but also clearly identify the limitations of our study. The small subject sample, especially with regard to the measurements with the whole-head-system, obviously implies that conclusions based on the data are preliminary and need further evidence through studies with additional subjects. Furthermore in those studies additional tasks that control for cognitive demands like working memory are needed. A fundamental limitation of the approach we have followed is the reliance on the average signal. We have demonstrated that brain activations to repeated similar stimuli vary from trial to trial, and we have developed techniques to map the activity in single trials [35,36]. We have started from the average signal because we wanted to relate as much as possible to earlier works which almost exclusively rely on the average signal. We are now processing the same data in single trials and studying the responses from individual emotional expressions (e.g., fear, surprise, etc.); the single trial analysis of face affect recognition will be reported elsewhere.

In summary, our results have provided evidence that recognition of facial expressions of emotion is maintained by a network of brain regions, that is constituted not only by the activation of a spatial pattern of regions but is also based on a relatively consistent pattern in time. Particularly the observed reactivations of brain regions might help to understand how the same neural substrate is involved in different psychologically defined functions by participating

in different transitory activated neural networks. Further studies are needed to determine whether this interpretation proves to be correct, and those that investigate the interplay between brain regions. MEG is well equipped to tackle these important questions in brain research.

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